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THE IMPACT OF THE SOIL ENVIRONMENT ON THE GROWTH OF ROOT SYSTEMS

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McMichael B. L. and Quisenberry J. E. *The impact of the soil environment on the growth of root systems.* Environmental and Experimental Botany **33,** 53–61, 1993.—There are numerous environmental factors that can influence the growth and function of plant root systems. The impact of some of the major soil-related factors such as soil temperature, soil water, soil air, soil strength, and soil nutrient supply on the development of roots is reviewed. Emphasis has been placed on the interaction of these factors with each other and with the genetic diversity inherent in plant roots in determining the impact of the soil environment on root growth and ultimately on plant productivity.

Key words: Cotton, root length, root density, strength, temperature, water.

INTRODUCTION

The growth and development of the root system are under genetic control but may be modified extensively by the environment. It has been shown in a number of recent studies that, for a variety of species, variability exists in the development of root length and in the initiation and growth of branch roots.[23,38,40,41] For example, Quisenberry *et al.*[47] showed significant differences in the development of taproot length and number of lateral roots in 35-day-old cotton plants, while others[8,32] have shown that there were varietal differences in root growth across several environments.

Changes in soil temperature, soil strength, composition of the soil atmosphere and soil water content are among the important environmental factors that can impact the growth and development of the root system.[38] Interactions can also occur between these and other factors both above and below ground (i.e. mycorrhizae, soil pH, soil nutrient status, photosynthesis, reproductive growth stage) to influence the development of the root system. Additional interactions with the diverse genetic backgrounds of plant species are also important in the determination of the growth of a particular root system across various environmental conditions.

This article focuses on discussions of the impact of the major soil environmental factors that influence root growth and also discusses to some extent the modification of the growth of root systems of different genetic material by the environment. Since the authors are more familiar with the cotton root system, many of the illustrations and discussions will pertain to the root system of this plant. In the case of most crop plants, however, similar responses can occur. For a more comprehensive study of other factors in the rhizosphere that influence root growth, such as mycorrhizae, the reader is directed to the excellent reviews by SYLVIA[54] and MUKERJI.[42]

MAJOR SOIL-RELATED FACTORS IMPACTING ROOT GROWTH

Most of the factors that directly affect root growth are soil related. These factors, as previously indicated, include soil strength, soil water, soil temperature, and composition of soil atmosphere. Wherever data are available, the impact of these factors on both morphological and functional changes in root systems will be discussed.

Soil strength

The growth of roots through compacted layers such as plow pans or areas of high bulk density can present significant problems in many crop-growing areas. Studies with penetrometer devices have indicated that as soil resistance increases root elongation rates tend to decrease[46,61] (Fig. 1). The decrease in elongation may mean that the plant can extract water and nutrients from only a limited soil volume since depth of rooting would be impaired. WANJURA and BUXTON[63] showed that the growth of both shoots (hypocotyls) and roots (radicles) of young plants were reduced by increased soil strength. GRIMES *et al.*[24] showed that a penetrometer resistance of 1.6 MPa at soil

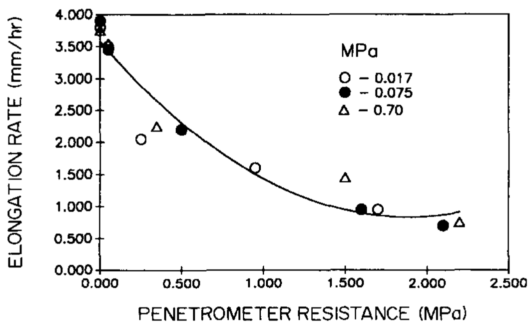

FIG. 1. The effect of penetrometer resistance at three levels of soil water potential (MPa) on the mean rate of cotton root elongation. (From H. M. TAYLOR and L. F. RATLIFF, Root elongation rates of cotton and peanuts as a function of soil strength and soil water content. *Soil Sci.* **108,** No. 2: 113–119, © Williams & Wilkins, 1969.[61])

volumetric water contents of near field capacity was sufficient to reduce rooting density of plum trees to about 50% of that in non-compacted soil. TARDIEU[55] showed that water extraction of maize roots was about half in an inter-row wheel-compacted zone compared to a non-compacted inter-row. Rooting density was also significantly lower in the compacted zone. CARR and DODDS[15] showed that small differences in soil bulk density had a significant effect on the rooting of lettuce.

There is some evidence that the morphology of the root system can change as a result of the roots growing in high-strength soil. TAYLOR and GARDNER[57] showed that root diameters were low in plants grown in high-strength soil which may have been due to smaller xylem and phloem cells as shown to be the case in other studies.[37] Genetic differences in the ability of root systems to grow into compacted layers are not well documented, particularly within a species. TAYLOR and RATLIFF[61] showed that peanut roots were less sensitive to increased soil strength than cotton roots. However, SHIERLAW and ALSTON[51] could detect no differences in the ability of annual ryegrass and maize to penetrate compacted zones. BENNIE[6] suggested that the relative decrease in rooting into a compacted zone is the same for most species and that the main differences which occur are related to the ability of the plant to produce branch roots in uncompacted layers. It has also been suggested that much of the observed difference may be hormone mediated.[49]

Soil temperature

The influence of changes in soil temperature on the growth of root systems has been documented for a number of species. The temperature of the soil, in general, is lower than that of the air and is less subject to rapid change, particularly at lower depths. It appears from several studies that there is an optimum temperature range for maximum root growth for all plant species. In general, the growth of roots tends to increase with an increase in soil temperature until the optimum temperature is reached, with a decrease then occurring as temperatures rise above the optimum range. ABBAS AL-ANI and HAY[1] showed that root extension rates increased significantly for each 10°C rise in temperature. It has been shown, for example, that the optimum soil tem-

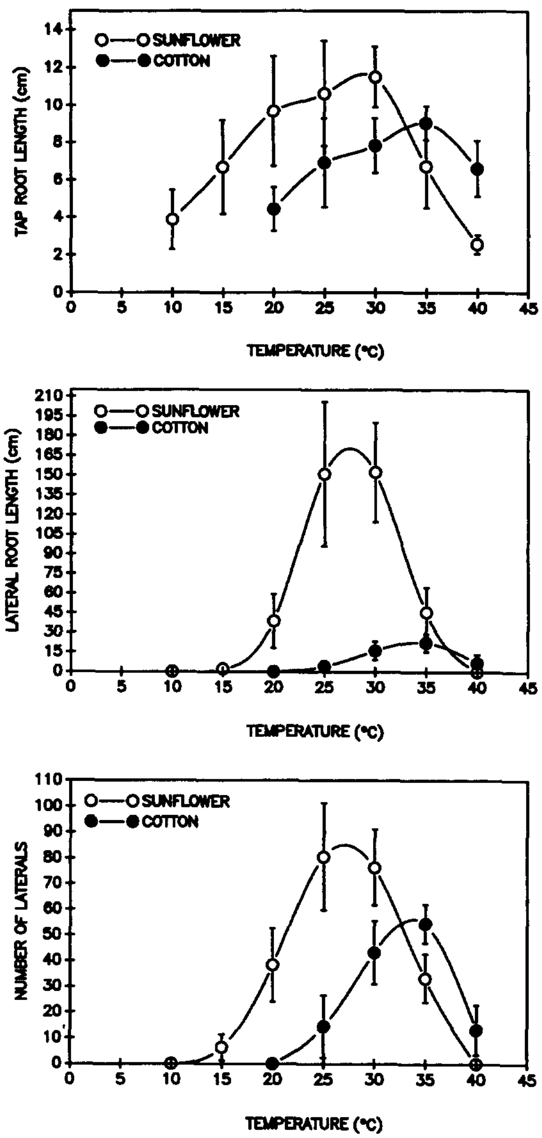

FIG. 2. Development of root systems of 10-day-old cotton and sunflower seedlings as a function of temperature. (McMICHAEL, unpublished data.[39])

perature range for the growth of cotton roots is between 28 and 35°C[39,46,58] (Fig. 2). In contrast, the optimum temperature for sunflower root growth was found to be in the range of 23–25°C[39] (Fig. 2). The optimum temperature for many forage legumes was shown to be even lower.[12,23] In the case of sunflower vs cotton, field studies

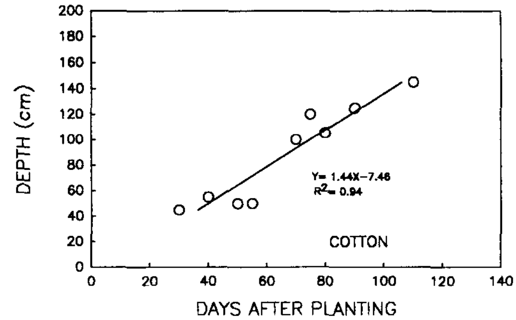

FIG. 3. Mean depth of rooting as a function of days after planting for field-grown cotton root systems. (McMICHAEL, unpublished data.[39])

using minirhizotrons for measuring rooting depth over time have shown that for similar soil conditions the sunflower roots grew at a faster rate than the cotton. This may be a manifestation of the different sensitivities of the roots to the same soil temperatures[39] (compare Figs 3 and 4).

When the soil temperature deviates significantly from the optimum a number of things may occur. At low temperatures the growth of the roots may be reduced and less branching can occur.[13] Water uptake can be reduced[44] and nutrient uptake can change.[45] CUMBUS and NYE[18] showed that in rape the concentration of nitrogen in the shoots was little affected by the root temperature but that the highest growth was associated with the highest nitrate depletion at root temperatures of 25–30°C. Other changes such as death of the root cortex,[16] accumulation of sugars,[26] and wilting[7] can occur when roots

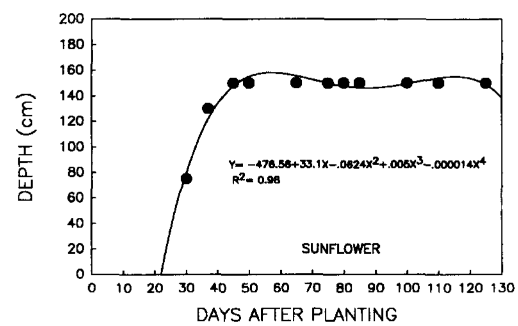

FIG. 4. Mean depth of rooting as a function of days after planting for field-grown sunflower root systems. (McMICHAEL, unpublished data.[39])

are exposed to low soil temperatures. The exposure of roots to higher than optimum temperatures can also have an adverse effect on the growth and development of the root system. Both elongation rates[2,61] and enzymatic activities[44] are reduced, while branching may be increased in some cases.[44]

There is also a body of evidence that indicates genetic variability in response to changes in temperature both between and within species. Brar *et al.*[11] showed that the temperature for optimum emergence and growth between a number of forage legumes was significantly different (Fig. 5). McMichael[41] has shown that there are differences in the temperature response of seedlings of a number of exotic cotton accessions in terms of primary and lateral root development. Quisenberry *et al.*[47] also showed similar differences in older plants. Heinrichs and Nielsen[29] showed differences in root growth of 20 alfalfa varieties in response to different soil temperatures. The differential response of cotton and sunflower seedlings (Fig. 2) is also an example of genotype × environment interaction.

The exact mechanism(s) of the response of roots to different soil temperatures has not been determined. Some researchers contend that changes in protoplasmic resistance can account for the observed responses, particularly the reduction in water uptake.[9] Others have indicated that the

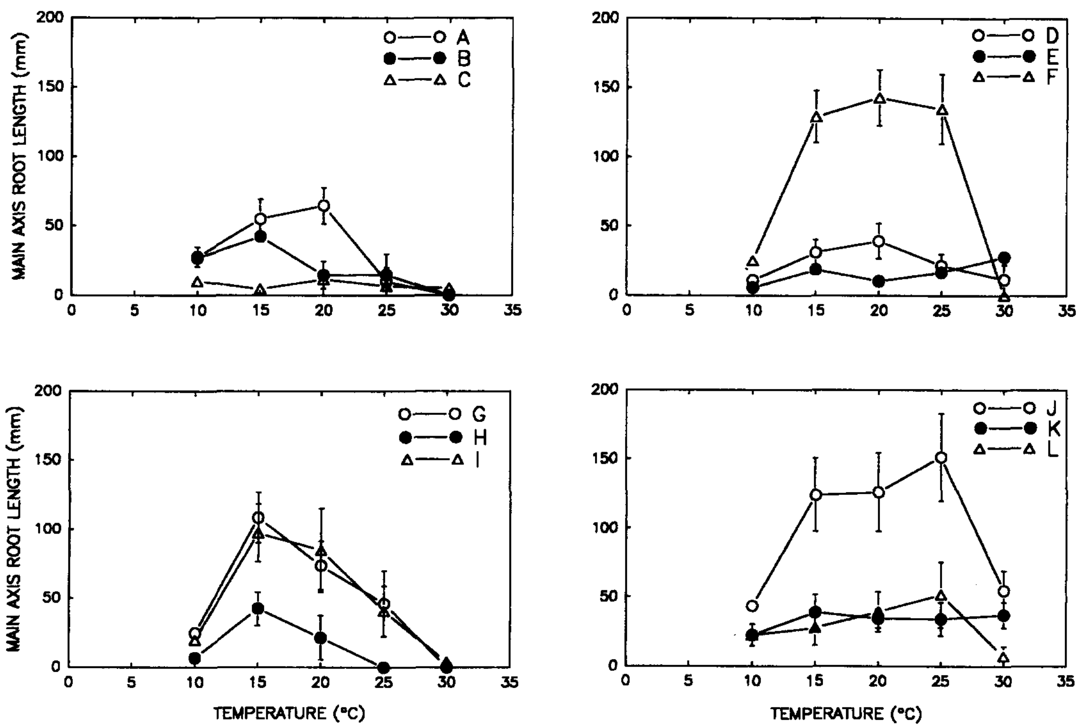

Fig. 5. Mean length (±S.E.) of main root axis of 10-day-old forage legumes as a function of temperature. (A) *Medicago rugosa* Desr. cv. Paraponto gama medic; (B) *Trifolium subterraneum* L. cv. Mt. Barker subterranean clover; (C) *Trifolium incarnatum* L. cv. Chief crimson clover; (D) *Trifolium pratense* L. cv. Kenstar red clover; (E) *Vicia sativa* × *Vicia serratifolia* Jacq. cv. Vangard vetch; (F) *Vicia grandiflora* Scop. cv. Woodford vetch; (G) *Pisum sativum* subsp. *arvense* (L.) Poir cv. Austrian winter peas; (H) *Medicago sativa* L. cv. Maxidor alfalfa; (I) *Trifolium vesiculosum* Savi cv. Amclo arrowleaf clover; (J) *Vicia sativa* × *Vicia corduta* Wulf. cv. Cahaba white vetch; (K) *Vicia villosa* L. cv. Hairy vetch; (L) *Onobrychis viciifolia* Scop. cv. Eski sanfoin. (From Brar *et al.*, *Agron J.* 1990;[11] used with permission.)

rate of cell division is reduced at the low temperatures and that as the temperature rises the time required for additional cell division is reduced.[4] Future research should shed more light on the nature of these responses.

Soil water

The water content of the soil can have a direct influence on the growth rate and distribution of roots. Rooting depth and rooting density may increase in a drying soil[33] (Fig. 6) and root elongation rates may be significantly decreased.[56] There also may or may not be significant alterations in root activity as the soil dries since root proliferation may occur at lower depths to maintain water uptake rates.[60] JORDAN[31] observed that rooting densities could decrease to as low as 0.2 cm/cm^3 and still effectively extract water. Water uptake rates were shown to increase with increased rooting densities in wheat plants depending on root age and soil water status.[50] MCMICHAEL[39] observed that rooting densities increased significantly at lower depths and decreased in upper soil layers in several commercial cotton varieties when the soil was allowed to dry. TAYLOR and KLEPPER[60] showed that root length did not increase in a soil layer when the water content of that layer fell below 0.06 cm^3/cm^3 equivalent to a soil water potential of about -0.1 MPa.

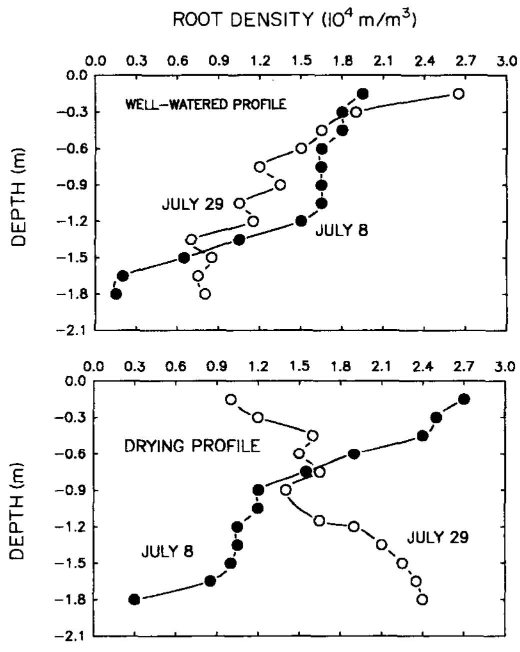

FIG. 6. Mean root length density profiles on two dates after planting. One profile was well watered (top) and one was allowed to dry (bottom). (From KLEPPER *et al.*, *Agron. J.* 1973;[33] used with permission.)

The effectiveness of roots to extract water as soil water is depleted appears to be rather constant in some instances. TAYLOR and KLEPPER[59] showed that water extraction per unit root length in cotton does not change with depth. In contrast, however, STONE *et al.*[53] indicated that in soybeans the depletion effectiveness, defined as cm^3 of water per g of root per day, was greatest at lower depths, presumably due to younger roots being in wetter soil. They also concluded that at any given time a small portion of the root system could be responsible for a large part of the total water uptake by the plant.

Changes in soil water potential can have a significant impact on the activity of root systems. LASCANO and VAN BAVEL[35] showed that the water uptake by the root system is proportional to the rooting density in a particular layer and the difference between the water potential of that layer and the overall mean leaf water potential. This approach was adequate to explain the water uptake by cotton roots divided over a wet and dry soil environment. HEATHERLEY[28] showed, in experiments where soybeans were grown in containers in which the bottom portion of the soil profile was kept relatively moist (soil water potentials of -0.02 to -0.04 MPa) and the top portion of the soil was allowed to dry to various soil water potentials, that the root dry weight accumulation was higher in the lower portion of the profile when the top portion was allowed to dry to -0.05 to -0.07 MPa. NEWMAN[43] showed that root growth in flax decreased at soil water potentials of -0.7 MPa, but that some root growth occurred in soil drier than -2.0 MPa.

Interactions may occur between the soil water status and nutrient supply to affect root growth. BARRACLOUGH *et al.*[5] showed that drought in the upper portion of the soil profile severely reduced root growth in that zone, but root growth was stimulated at lower depths when moisture and nitrogen were present. VEGH[62] also showed that the uptake of phosphorus was highly dependent on the soil moisture and that higher amounts of available nutrients resulted in greater root elongation when moisture was adequate.

There is also some evidence to suggest that genetic differences exist in the response of roots to changes in soil water. CUTFORTH *et al.*[19] showed that root growth in one variety of corn (Pioneer 3995) was less sensitive to water stress than two other varieties that were tested. There was also an interaction with temperature which indicated that sensitivity to water content decreased with decreasing soil temperature. QUISENBERRY *et al.*[47] showed that there was significant variability in root growth of a number of cotton genotypes that was positively associated with shoot dry weights in dryland situations. They also indicated that root growth potentials appeared to be important traits in the adaptation of cotton to water-limited conditions.

Therefore, changes in soil water content and soil water potential may change rooting patterns and root activity in relation to top growth and have a significant impact on plant productivity.

Soil nutrient status

There have been numerous studies conducted concerning the uptake of nutrients by plant roots and the impact on productivity.[3,36] Many of these studies have focused on the pathways of nutrient transport, and the interactions between nutrients and changes in absorption rates as a function of soil temperature and water status.[20,48] Obviously, the soil water status plays a major role in the utilization of nutrients by plant roots since the water is the carrier of nutrients to the root surfaces. Therefore, changes in soil water status directly impact root–nutrient relationships. VEGH[62] showed that, under adequate soil water conditions, changes in nutrient supply had little effect on root length of barley plants. However, when water was limiting, increasing the nutrient supply increased the total root surface area. Some studies have been conducted, however, relating soil nutrient status to the growth and development of the root system itself. DREW *et al.*[21] showed that the concentration of nitrate in the soil had a significant effect on lateral root development in barley. There was an increase in lateral rooting in zones where nitrate concentrations were increased from 0.01 to 1.0 mM. COOKE[17] showed similar results with pea roots in response to phosphorus and potassium placement. There is also some evidence that different genotypes respond differently to soil nutrient status. HACKETT[27] reported that the root systems of different varieties of barley showed different morphological characteristics as a result of differences in nutrient levels, particularly phosphorus and potassium deficiencies.

Soil aeration

The composition of the soil atmosphere may significantly reduce or enhance the development of roots depending on the concentrations of the soil gases. In general, the soil air is about 79% N_2, 20% O_2, and less than 1% CO_2 at a depth of about 15–20 cm.[52] These concentrations can vary from as little as 5% O_2 to as much as 15–20% CO_2[14] and are influenced by other environmental factors such as soil temperature and soil water status.[52]

The roots of some species respond differently to changes in the composition of the soil atmosphere. The growth of cotton roots, for example, does not seem to be hindered by CO_2 levels in the soil that would severely reduce root growth in other crops.[34] On the other hand, the growth of cotton roots is highly sensitive to changes in soil O_2 concentrations. Elongation rates of the taproot, for example, were reduced when the root system was exposed to 5% O_2, and roots were killed within 3 hr after the soil atmosphere was purged of oxygen.[30] WHITNEY[64] reported that water uptake by cotton roots, as well as root systems of other crops, was reduced either by toxic effects of the increased CO_2 reducing root permeability or reduction in respiration rates brought about by the low O_2 concentrations.

Flooding conditions are prevalent in some soils that can severely reduce root function. BOX[10] reported that reduced O_2 diffusion rates significantly decreased the number of roots and the depth of rooting of wheat plants grown on waterlogged soils of the Southeastern U.S. DREW and STOLZY[22] indicated in their review concerning oxygen stress, that the root systems of some species may adapt to low oxygen conditions by forming lenticels or aerenchyma cells to facilitate gas exchange. They also indicated that there may be metabolic adaptation as well as changed enzyme systems to respond to more anaerobic conditions. GRINIEVA[25] also observed similar adaptation responses in flooded root systems of *Zea mays*.

CONCLUSIONS

We have discussed some of the major soil-related factors that impact root growth in plants and how these factors may interact to influence not only root development but also productivity. One important aspect that has been somewhat overlooked at times is the influence of the genetic component for root growth and how the genetic potential for root development may be modified by the environment. Some species, and even some genotypes within the same species, may respond differently to changes in the soil environment which not only affect water and nutrient uptake by the root systems but ultimately influence the productivity of the plant. Future research should aim at a better understanding of the interaction of the root system with its environment in efforts to increase plant performance under a wide range of environmental conditions.

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